

FURTHER STUDIES IN THE BEHAVIOR OF COMMENSAL POLYCHAETES

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To date a number of studies have been made on the response specificity of commensal polychaetes (Davenport, 1950, 1953a, 1953b; Davenport and Hickok, 1951; Bartel and Davenport, 1956). In these studies a number of techniques to discern the presence of chemical responses to host have been employed. The subject of specificity and behavior in animal partnerships has recently been reviewed (Davenport, 1955).

During the summer of 1956 further investigations of the behavior of a number of polychaete commensals were conducted at the Friday Harbor Laboratories of the University of Washington. The authors wish to express their appreciation to the Director and staff of the Laboratories for their continued interest and support in these researches. The studies are currently continuing in the Marine Biological Laboratory of Santa Barbara College and have been supported since 1955 by a contract from the Office of Naval Research.

The preliminary investigations cited above had indicated the necessity to compare the behavior of populations of single species of facultative and obligate commensals of diverse host-habit, and to determine whether these populations showed different response specificity. The following studies were directed to that end.

THE FACULTATIVE COMMENSAL *PODARKE PUGETTENSIS* JOHNSON

Material

The hesionid polychaete *Podarke pugettensis* provides a most interesting subject for behavioral studies. The worm is a facultative commensal, and there appears to be no discernible morphological difference between free-living and commensal members of the species. In the free state the species occurs in great numbers under certain conditions; one may at times collect as many as 15–20 per square yard on the mudflats of Garrison Bay, San Juan Island, Washington. In the Southern California region it may be collected as it settles out of the plankton by suspending open-mouth jars under floats in San Pedro Harbor (D. J. Reish, personal communication), while numbers of adults may be taken by scraping the under surface of floats in the same locality and in Santa Barbara Harbor. It may also be collected by removing large pieces of the growth from pilings, where it occurs near the wood surface deep among the shells of the gastropod *Aletes* and the pelecypod *Chama*. It occurs among the byssus threads of *Mytilus* on pilings. Under these conditions the worms do not appear to be associated with any particular organism, but they certainly seem to thrive in environments of extremely rich organic content. Free-living individuals will be found sporadically in many sorts of environments, particularly where there is rich mud, in the inter-tidal and subtidal. During the summer of 1956 ripe

swarming adults were taken at the night light at Friday Harbor for the first time; whether these had been free-living or had come from hosts could not be determined. Swarming has never been observed by us in Southern California.

In California, these worms are commonly associated with the web-star *Patiria miniata* (Brandt), on one individual of which as many as 15–20 may occur. In the Pacific Northwest they are equally common on the mud-star *Luidia foliolata* Grube. There may be considerable variation in the size of worms on both hosts, indicating repetitive colonization by different age classes. In the Puget Sound-Vancouver Island region they may occur on the cushion-star *Pteraster tesselatus* Ives and together with *Nereis cyclurus* Harrington commensal with hermit crabs (Berkeley and Berkeley, 1948). Steinbeck and Ricketts (1941) list the species as commensal with the starfish *Oreaster occidentalis* Verrill in the Gulf of California. That it may occur occasionally with *Pisaster ochraceus* (Brandt) is indicated by a single specimen in the collection of Dr. Olga Hartman, taken by Dr. S. F. Light at Dillon Beach, California. In spite of examining numerous specimens of the common starfish, from Puget Sound to Southern California, we have never found commensal polychaetes of any sort associated with it; there would appear to be a likelihood that the above case was fortuitous.

Method of investigating responses

A.

A choice-apparatus has been designed for the investigation of the possible role of chemical attractants in the regulation of partnerships, such as that between *Podarke* and *Patiria*, in which we have been unable to demonstrate in the individual commensal partner any sharply defined, objectively recordable response to the host (Bartel and Davenport, 1956). The apparatus consists of an aquarium with a central chamber surrounded by and connected by passages with six radially arranged chambers. It may be constructed out of latex as described in the above citation. Our use of the apparatus was as described except that a cover of plywood was added to reduce the possible effects of light. The latter factor was eliminated from consideration in any series of tests by the random selection of test chambers from the possible six. In all the experiments using this apparatus described below, the presence or absence of an attractant factor in one of the chambers among the radial six (the "critical" chamber) is indicated when probabilities, using the null hypothesis that distribution into the six chambers is the result of chance, indicate that either a significant or insignificant number of worms have moved from the central chamber into the critical chamber. Tests averaged from 8 to 12 hours.

Between each test in a series in any experiment the apparatus was washed. Host animals were generally housed during tests directly in one of the radial chambers, but in certain tests indicated below, when host animals were very large, they were housed in a clean, redwood and glass aquarium and the water therefrom siphoned into a radial chamber of the choice-apparatus.

B.

Prior to employing the above described choice-apparatus, Bartel and Davenport (1956) had found, by the simple expedient of placing in dishes large numbers of free-living and commensal *Podarke* together with *Patiria*, that toward this host

there is a marked difference in behavior in the two populations; the commensals gathered on the star while none of the free-living worms did. It seemed wise to repeat this experiment in Puget Sound, using both the free-living worms and those commensal with the common host of that region, *Luidia foliolata*. As an experimental animal in behavior studies this starfish presents difficulties; it readily autotomizes its arms when handled or placed in a confined space and hence is not well suited to the latex choice-apparatus. At the same time it is so large that one cannot readily place it in a dish or tray with commensals. We therefore employed a large cement water table (internal dimensions $3' \times 5' \times 3''$) in which the starfish could wander freely and "pick up" commensals or in which one could confine the star to a limited space so that the commensals had to "find" it (Fig. 1). In order to so confine the starfish we simply placed a plywood "T" in the table as shown, which would allow free movement of water or worms under its parts but which would

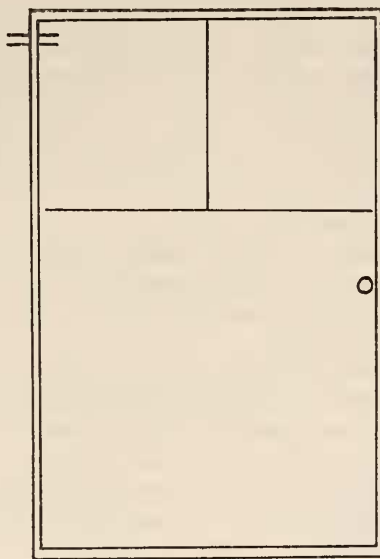


FIGURE 1. Plan of water table.

trap the star in one corner. Water was introduced at a very slow flow in one corner and drained out at the point shown. One introduced experimental worms at random at the lower end of the table.

This apparatus lent itself well to the study of the specificity of response in partnerships in which evidence for a chemical attraction effective at a considerable distance from the host had already been presented (*Arctonö-Evasterias*, etc.—Davenport, 1950), and also made it possible to conduct tests concurrently with those using the latex apparatus, likewise testing the responses of a large sample of worms in a single test run.

Experiments

Experiment No. 1. Will commensal worms gather on the host *Luidia* when both have the freedom of the water table?

After a time duration of approximately eight hours, 23 out of 36 introduced worms (59%) had moved onto the starfish.

Experiment No. 2. Will commensals, introduced at random at the lower end of the table, find the host if it is trapped at the opposite end?

After a time duration of approximately nine hours, out of 23 worms introduced 13 had found the starfish (56%).

Experiment No. 3. Will free-living *Podarke* (Garrison Bay) gather on *Luidia* when both have the freedom of the water table?

After a time duration of approximately eight hours, out of 32 worms introduced none had moved onto the starfish.

Experiment No. 4. Can an attraction for commensal worms be demonstrated in the latex choice-apparatus if water is siphoned from a large aquarium containing the host *Luidia* into one of the six radial chambers?

Six *Luidia* were placed in a large redwood aquarium and three tests followed a control. In the control test with no starfish water in the system, 18 out of 23 worms made a choice and the distribution in the radial chambers was random. In the first test to starfish water, out of 25 worms introduced, 23 made a choice and of the 23, 14 entered the critical chamber ($P < .001$). In the second test all of 20 worms made a choice and of these 8 entered the critical chamber ($P < .01$). In the final test out of 25 worms 11 made a choice, of which 9 entered the critical chamber ($P < .001$).

It is clear that an attraction can be demonstrated with the *Podarke-Luidia* partnership in the latex apparatus. The above data compare very well with those obtained by Bartel and Davenport (1956) with the *Podarke-Patiria* partnership in California, in which two tests gave probabilities of $< .001$ (24 out of 68 and 23 out of 53 entering the critical chamber).

Experiment No. 5. Are free-living worms attracted to a radial chamber into which water from an aquarium containing *Luidia* is siphoned?

In a control test with no starfish water in the system, 16 out of 22 worms made a choice and the distribution was random. In four tests in which 15 out of 25, 16 out of 20, 17 out of 20 and 17 out of 24 made a choice when starfish water was in one of the chambers, the distribution was still purely random. In a single test against starfish water when 16 out of 24 worms made a choice, 8 entered the critical chamber ($P < .01$).

Since the above results were not consistent, further tests were indicated to determine whether or not the release of metabolites in test chambers may occasionally cause free-living worms to distribute themselves unequally in the choice-apparatus, in spite of the fact that under conditions more nearly approaching natural ones, they do not gather on *Luidia* (Experiment No. 3 above).

Experiment No. 6. Can closer propinquity to starfish (and therefore possibly greater concentration of metabolites) perhaps be the answer to the unequal distribution that may occur when free-living worms are tested in the choice-apparatus against *Luidia*? With considerable difficulty a single small *Luidia* was obtained for testing and one test completed with the starfish directly in one of the radial chambers before it autotomized its arms. In this test when 23 out of 30 worms made a choice, 8 entered the critical chamber ($P < .01$).

Experiment No. 7. A further series of tests were conducted at a later date to see whether free-living worms from a different environment than those used in Experiments 5 and 6 might distribute themselves in a non-random fashion when a host was in the system. Free-living *Podarke* from harbor floats in Santa Barbara were tested against the host starfish of California, *Patiria miniata*. In four out of five tests of this kind the distribution was random, but in one, when 19 out of 27 worms made a choice, 10 entered the critical chamber ($P < .001$).

Experiments 5, 6 and 7 have all given an indication that under certain conditions the behavior of free-living worms may be so affected by the presence of a host starfish in the system (perhaps by some metabolite) that their distribution will be non-random. However, they certainly do not respond positively as consistently as their commensal relatives.

Experiment No. 8. It has been demonstrated that commensal *Podarke* show a positive response to the host *Luidia* (Experiments 1, 2, and 4). Will worms from *Luidia* respond to the alternate host *Pteraster tessellatus*?

In two tests in which water from a redwood aquarium containing a single large *Pteraster* was siphoned into one of the six chambers, samples of 19 and 20 worms distributed themselves in a random fashion. But when a smaller *Pteraster* was placed in a radial chamber directly, in one test when 18 out of 23 worms made a choice, 9 entered the critical chamber ($P < .01$) and in the second test when 31 out of 36 worms made a choice, 16 entered the critical chamber ($P < .001$).

Here again propinquity may be a factor, and perhaps the great secretion of mucus produced by handling this starfish may have been a factor in preventing a response in the first two tests, when the starfish was at a greater distance.

Experiment No. 9. How specific is the response of commensals from *Luidia* in the choice-apparatus? Will the commensals respond to non-host starfish?

In a test against *Mediaster aequalis* Stimpson, when 24 out of 31 worms made a choice, 9 entered the chamber containing the host ($P < .01$). In a test against *Pisaster ochraceus* (Brandt) when 9 out of 19 worms made a choice, 5 entered the critical chamber ($P < 1.0$) and in a test against *Evasterias troschelii* (Stimpson) when 17 out of 27 worms made a choice, 11 entered the critical chamber ($P < .001$).

Apparently no response specificity can be demonstrated in the latex choice apparatus when one tests *Podarke* commensal with *Luidia* in Puget Sound.

Experiment No. 10. Do California *Podarke* commensal with *Patiria* show a similar non-specific response in the latex choice-apparatus?

In a series of six control tests against the host alternated with tests against non-host stars, distributions giving probabilities of $< .001$ were obtained in five, while in one test the distribution was random. In the series of 15 tests against *P. ochraceus* (Brandt), *P. giganteus* (Stimpson), *Pycnopodia helianthoides* (Brandt) and *Dermasterias imbricata* (Grube), when samples of from 10 to 44 commensals were used in a single test, all but one test gave completely random distributions. In one test against *P. giganteus* 19 out of 33 worms making a choice entered the critical chamber ($P < .001$).

There would appear to be a marked difference in the response specificity demonstrable in the choice apparatus between worms commensal with *Luidia* in Puget Sound and worms commensal with *Patiria* in California, the latter demonstrating a greater specificity.

THE OBLIGATE COMMENSAL, *ARCTONOË FRAGILIS* (BAIRD)*Material and methods*

The polynoid commensal *Arctonoë fragilis* has been studied previously by the authors (citations above). In the first experiments in which it was demonstrated that a marine commensal would respond positively to sea water which housed its host, a Y-tube olfactometer was used, but no detailed studies of response-specificity were made. Such apparatus does not lend itself readily to investigations of specificity of response, since large samples of commensals cannot be tested at once. As it had already been demonstrated that these worms showed an "overt" response to sea water from their host even at a distance, there appeared to be no advantage in employing the latex choice-apparatus. The use of similar water-table tests as described above (Fig. 1) was in order.

A. fragilis has been listed as commensal by Pettibone (1953) with the following asteroid hosts: *Evasterias troschelii*; *Leptasterias aequalis* and *L. hexactis*; *Orthasterias koehleri*; *Pisaster ochraceus*; *Solaster dawsoni* and *Stylasterias foreri*. We collected and used in the experiments below a large number of worms commensal with *Evasterias*, a few with *Orthasterias* and one (?) with *Solaster dawsoni*. It is unfortunate that cross-specificity studies are made difficult by the fact that it is almost impossible to collect a working sample of commensals from any other host than *Evasterias*. The Berkeleys tell us that at Nanaimo large numbers of *Orthasterias koehleri* can be collected in the inter-tidal zone in winter and early spring; in summer they can only rarely be so collected. Our few specimens of *Orthasterias* were taken in dredges and with the aqualung. It may in fact be possible in the future to compare the behavior of populations of *A. fragilis* from *Evasterias* and *Orthasterias*, by conducting winter experiments. The value of making a thorough comparison of the behavior of two or more separate populations of a single commensal species which inhabits several hosts is obvious. The brief preliminary tests presented below give evidence that the results of such experiments would be most interesting.

Experiment No. 11. Prior to running cross-specificity tests with the two populations of *Arctonoë* available, it was necessary to run a control experiment to determine whether under the conditions of the water table, *Arctonoë fragilis* (commensal with *Evasterias*) would show a response to non-host stars. In four control tests against *Evasterias*, run in alternation with tests against non-host stars, fifteen worms were used in three and fourteen in one. Tests had a duration of not less than nine hours. In the first three 12 out of 15 (79.9%), 10 out of 15 (66.6%), and 10 out of 15 "found" the "trapped" host. In the one test using 14 worms, 13 "found" the host (92.8%). In single tests using fifteen worms against *Pisaster ochraceus*, *Luidia foliolata*, *Mediaster aequalis*, *Hippasteria spinosa* and *Dermasterias imbricata* no worms "found" or moved onto the "trapped" non-host.

Commensal *Arctonoë*, therefore, demonstrate a rather precise response specificity in the water-table.

Experiment No. 12. It appears that commensals from *Evasterias* do not, as one might expect, demonstrate in the water-table a response to stars with which the species is not associated, but what sort of behavior would the worms show in relation to alternate hosts? Will the worms, regardless of host habit, respond to alternate hosts?

To answer this question we presented mixed samples of *Arctonoë*, some from *Evasterias* and some from *Orthasterias koehleri*, with opportunities to "find" each host in the water table. Will each host "sort out" the correct commensals? Unfortunately, because of the above-mentioned difficulty of finding *Orthasterias* we were able to collect only two specimens of *Arctonoë* from this host. In the following experiments these worms were lightly stained in indulin in order to distinguish them from the sample collected from *Evasterias*.

In a series of three water-table tests of this mixed population against *Evasterias* a total sample of 16 worms were used in each. In the first two tests 15 *Evasterias* commensals "ran against" one *Orthasterias* commensal. At the end of nine hours in both tests 10 (75%) of the *Evasterias* commensals had "found" their host while the single *Orthasterias* commensal was still wandering free. In the third test 14 *Evasterias* commensals were "run against" two *Orthasterias* commensals. At the end of nine hours all but one of the *Evasterias* commensals had "found" the host while the two *Orthasterias* commensals were still wandering free.

In two tests against *Orthasterias* a mixed sample of 15 worms was used in the first and of 17 worms in the second. In the first, out of 14 worms from *Evasterias* 13 were still wandering free after nine hours, while the single *Orthasterias* worm had "found" its host. In the second test at the end of the same time, out of 15 *Evasterias* worms none had moved onto the *Orthasterias*, while of the two *Orthasterias* worms, one had "found" the host.

These preliminary experiments against alternate hosts were conducted with a much smaller sample of worms than one would desire and it is hoped that at some time such tests can be repeated with balanced samples. But the tests give an indication of what may be a significant fact. There may, if such responses are not conditioned during development, be good physiological or behavioral races inhabiting different hosts within single commensal polychaete species. That this may be the case was further indicated by a brief experiment in which we tested a mixed population from *Evasterias* and *Solaster*. Accurate identification of the three species of *Solaster* with their two commensal species of *Arctonoë* (*S. stimpsoni* and *S. endeca* with *A. vittata* and *S. dawsoni* with *A. fragilis*), may be difficult. This is particularly true in the case of the worms, in which two species inhabiting closely related hosts may resemble each other greatly; identification can at times only be made by dissection which renders the animals useless for behavior experiments. However, we believe our identification of a single *A. fragilis* on *S. dawsoni* to be correct. When a mixed population consisting of 16 *A. fragilis*, one from *Solaster* and 15 from *Evasterias*, were tested in the water-table against *Solaster*, not one of the *Evasterias* worms moved to the star and yet the single *Solaster* commensal quickly "found" its host.

THE OBLIGATE COMMENSAL ARCTONOË VITTATA (GRUBE)

Material and methods

The polynoid *Arctonoë vittata*, closely related to *A. fragilis*, has perhaps the most interesting variation in host-habit of all the members of the genus. It colonizes certain asteroids, amphineurans, gastropods and polychaetes and within these groups shows a rather precise specificity (Pettibone, 1953). For this reason one might suppose that there could hardly be a commensal better suited to studies of response

specificity. Unfortunately, however, as with *Arctonoë fragilis*, it is very difficult to obtain large enough numbers of commensals from each host to make good studies of cross-specificity. In addition to the difficulty in collecting diverse populations of this commensal, one faces the problem of the general inactivity of the worm, which makes studies using a Y-tube or an open water-table tedious in the extreme. It was found, however, that a sample of animals distributed themselves well overnight in the latex choice-apparatus. The following questions were asked and to a certain extent answered, using a single population of worms from the key-hole limpet *Diadora* in the latex apparatus, according to the technique described above.

Experiment No. 13. Will commensals from *Diadora* show a response to the host in the choice-apparatus?

In eight tests samples of from 11 to 29 worms were tested against a group of six limpets in a radial chamber. In two of the eight tests the worms distributed themselves in a random fashion but in six of the tests enough worms chose the critical chamber to give probabilities of $< .001$, $< .01$, < 1.0 , < 1.0 , $< .001$, and $< .1$.

Experiment No. 14. Do worms commensal with *Diadora* show a response to alternate hosts? Sample alternate hosts tested were the starfish *Luidia foliolata* Grube, *Solaster stimpsoni* Verrill, and *Dermasterias imbricata* Grube; the chiton *Cryptochiton stelleri* Middendorf; and the gastropods *Acmaea mitra* Eschscholtz and *Fusitriton oregonense* (Redfield). Large hosts (*Luidia*, *Solaster*, *Dermasterias*, *Cryptochiton*) were housed in a clean redwood aquarium and the water siphoned from this into one of the radial chambers of the choice-apparatus. Small hosts (*Acmaea*, *Fusitriton*, small *Cryptochiton* and *Dermasterias*) were placed directly in a radial chamber.

In thirteen tests against these alternate hosts using samples in each of from 13 to 27 commensals the worms distributed themselves in the radial chambers in a random fashion. In a single test of the three against *Fusitriton*, when 20 worms made a choice, 8 entered the critical chamber ($P < .1$), while in the other two tests the distribution, although in both cases the greatest number of worms making a choice entered the critical chamber, gave probabilities $> .1$.

This series of tests indicates that the population of worms commensal with *Diadora* shows under these experimental conditions a rather precise response specificity. Unfortunately, the time duration of this experiment precluded our going further than analyzing the response to an array of available hosts. Certainly, a longer series of tests should be made against *Fusitriton* to determine whether toward this animal, which in some places occupies the identical environment from which the host *Diadora* may be collected, the worms show a constant response.

DISCUSSION

Since the initiation of the study of the specificity of response of polychaete commensals in the summer of 1949, a number of different forms have been investigated. It has been our continued aim to try to correlate this response specificity with the known host specificity of the species or races. In our effort to make comparisons we have been continually faced with difficulties, some of which have been insurmountable. Among these is the fact that it is extremely difficult to collect large enough samples of worms for such studies in those most interesting species which show within themselves a diversity of host habit; in most such species the worms

will, in one locality, occur commonly on one host but very rarely on others. A difficulty encountered in making comparisons between the behavior of different species has been that, as one might expect, not all species exhibit the same sort of response, some showing as individuals a marked or overt response to factors from the host coming from a distance and others merely "accumulating" on or near the host after a passage of time. With such forms as the latter it has been necessary to design special techniques quite different from those used in studies on the former to discern whether or not there is in actuality any response to chemical factors coming from the host. The use of entirely different techniques has made a comparison of results difficult. Some differences in response specificity may turn out to be more apparent than real when some technique has been developed which lends itself equally well to the study of the responses of forms which appear to differ in behavior. Recently we have begun an analysis of the behavior of individual polychaete commensals when under the influence of host factor, using apparatus which may give us some truly comparable data even when studying animals of greatly differing activity or sensitivity.

However, it may be possible at this time, in spite of the above-mentioned difficulties, to make some brief general observations on response specificity in commensal polychaetes.

There would appear to be different categories of response specificity. There is a range of behavior, from the sort which is exhibited by species or populations within species that respond to their host alone, to the sort in which the commensals appear to have no chemical discernment and respond, at least under experimental conditions, to many non-host animals. Specificity of host habit is by no means an indication of specificity of response in experimental apparatus. As an example of the first category which exhibits precise response we have *Arctonoë fragilis* and its behavior in relation to *Evasterias*, *Orthasterias* and *Solaster*. But there are also species in which populations from one host may give a similar precise response to some, but not necessarily all, alternate hosts, regardless of the absence of any taxonomic affinity between the hosts to which they do respond (*Harmothoë lunulata* from the brittle-star *Acrocnida brachiata* vs. its host and the alternate eunicid *Lycidice ninetta*—Davenport, 1953b). Among such species of diverse host habit there may be a population occurring on one of the array of hosts which responds to its host alone, in spite of the fact that other populations of the same species respond to several alternates (*Harmothoë lunulata* from *Leptosynapta inhaerens*). A further category consists of those species which respond with the same intensity to the known alternate hosts but with reduced intensity to a number of non-host relatives of their hosts (*Acholoë astericola* from *Astropecten irregularis* vs. its host and the alternate *Luidia ciliaris*, as well as non-host stars—Davenport, 1953a). Finally we have a category which, though somewhat unexplainable, can be demonstrated to exist even when using a standard technique. In some facultative commensals there appear to be populations (*Podarke* on *Patiria*) which show a precise response specificity to their host alone and others (*Podarke* on *Luidia*) which seem unable to discern the difference between their host and other non-host animals.

It is therefore quite apparent that it is pressing to determine, particularly in forms such as *Podarke*, whether responses are inherited or conditioned. Although it would seem difficult to imagine a mechanism whereby such a host response could be conditioned in forms such as *Podarke*, the early stages of which (in the labora-

tory) remain in the plankton for some 30 days, nevertheless only successful breeding and settling experiments will give us the answer.

SUMMARY

1. A new water-table test apparatus for the investigation of commensal response behavior is described.

2. Evidence is presented that the two populations of the facultative commensal *Podarke pugettensis* (Polychaeta: Hesionidae) which may be termed "commensal" and "free-living" differ markedly in their response to host animals, the commensal worms showing a strong tendency to respond positively to the host and the free-living worms not doing so.

3. Commensals with the starfish *Luidia* in Puget Sound appear to respond with almost equal intensity to other non-host animals (the response is not specific), while commensals of the star *Patiria* in Southern California show a more precise and specific response. This behavioral difference remains unexplained.

4. The behavior of three populations of the obligate commensal *Arctonoë fragilis* (Polychaeta: Polynoidae) was compared. Evidence is presented that each population (one commensal with the star *Evasterias*, one with the star *Orthasterias* and one with the star *Solaster*) shows a response to its host alone.

5. The response behavior of *Arctonoë vittata* (Polychaeta: Polynoidae), an obligate commensal of diverse habit, was investigated in relation to a number of its alternate hosts.

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